Shell form and habitat choice in Lymnaea

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Shell form and habitat choice in *Lymnaea*

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The shell form of aquatic gastropods can vary among closely-related species or populations according to the intensity of water movement in a habitat[1] or to other environmental factors.[2–4] Freshwater snails can also adapt to local conditions by altering life history traits.[5–8] There is evidence[9] that these differences are at least partly under genetic control in certain populations of *Lymnaea peregra*.

The shell morphology of *Lymnaea peregra* is very variable, though no differences amongst forms in internal anatomy have been found.[10,11] We consider here two forms, referred to as *peregra* and *ovata*, which are almost certainly different species.[12] Form *ovata* has a rather compact shell with a wide opening while *peregra* has a longish shell with a narrow opening. The shell form of *ovata* seems advantageous in running waters or on wave-washed shores, as it allows the expansion of a large foot which enables the animal to attach firmly to the substratum and so withstand strong water movement.[1,10,13] Form *peregra* seems better suited to drying conditions, because the snails can more easily retreat into the mud when a water body dries and their water loss is limited by the narrow opening, as in other lymnaeid species which live in temporarily drying waters.[14]

Both forms occur in the Seealpsee, an isolated lake in the Swiss Alps (1142m above sea level; longitude 9 24′ E, latitude 47 16′ N). This is unusual; different forms of *Lymnaea* are usually found in different, if close, water bodies.[12,15] There is a flat, muddy and vegetated shore in the south western end of the lake; otherwise the shore is mostly steeper and stony. The shallow area dries out at least once during the summer. Form *peregra* is only found in the shallow, drying area whereas *ovata* is common on the stony shores but also occurs in the shallow area. We examined the habitat choices of snails from two differing shore habitat types in a laboratory experiment by exposing them to a variety of water depths and substratum types.

Three categories of snail were used; *peregra* from the shallow area and *ovata* from both the shallow and deeper areas. Around 30 newly-collected animals, separated by category, were put into the centre of the water surface of a 100 × 50 × 50 cm tank which contained a 'staircase' of containers (Fig. 1). Each 'stair' was of two containers and there were five along the length of the tank; i.e. five different water depths were available to the snails. These ranged from almost no water to 40 cm depth. At each depth one container was filled with stony substratum and the other with muddy soil and a bunch of sedge; the water used was aged tap water but all substrata came from the Seealpsee. The arrangement of the two substratum types within a depth was randomly determined. There was no water movement in the tanks.

The experiment was replicated five times with snails collected from the lake one day before. The distribution of the snails over water depths and substratum types was recorded after 2 or 3 days in the tank. We therefore assume that the snails had made a stable habitat choice. Substrata were divided into 'hard substrata', which included tank and container walls as well as the stones themselves and 'vegetation and mud', which comprised sedge and muddy soil. Snails were re-released in the lake after the final replication.

Repeated measures analysis of variance was used to examine the habitat preferences of the snails.[16,17] The substratum types were nested within the depth categories, as each substratum was available at each depth. Both the effects of the substratum within depth by snail type and the depth by snail type interactions were significant (Table 1); making these the effects which should be interpreted.[18]

All snail types were approximately equally likely to be on the hard substratum but this was not the case for the vegetation and mud substratum (Fig. 2). Form *peregra* were most likely to be on the vegetation and mud, followed by *ovata* collected in the shallow area and then *ovata* from the stony shore, which was hardly ever found there. Although there was no strong pattern, *peregra* tended to prefer shallower depths and were commoner than both *ovata* types in the three shallowest depths (Fig. 3). However, *ovata* from the stony shore markedly preferred the deepest depths while *ovata* from the shallow area preferred somewhat intermediate depths. These habitat choices were consistent with the forms' field distributions. Lodge found no substratum preference by the *L.*

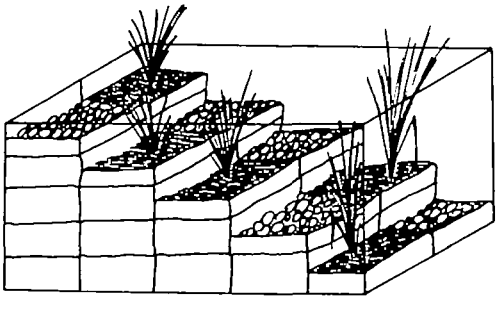

Figure 1. The experimental set-up.

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Table 1. The analysis of variance results for the habitat choice experiment

Source	Degrees of freedom	Mean square	*F*	*P*
Snail type	2	16.01	10.17	0.003
Residual	12	1.57		
Depth	4	8.19	4.04	0.007
Depth by snail type	8	9.21	4.55	<0.001
Residual	48	2.03		
Substratum within depth	5	12.25	5.77	<0.001
Substratum within depth by snail type	10	17.73	8.35	<0.001
Residual	60	2.12		

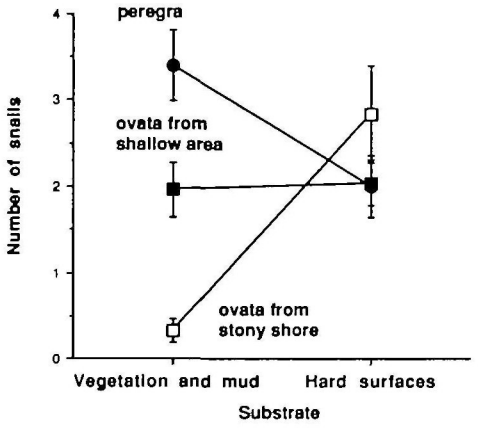

Figure 2. The substratum preferences (± SE) of each snail form in the laboratory experiment.

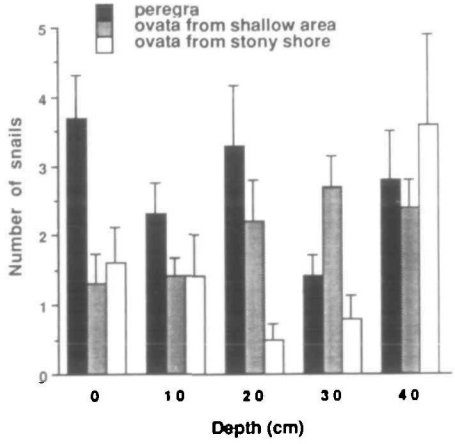

Figure 3. The depth preferences (+ SE) of each snail form in the laboratory experiment. At the shallowest depth the muddy soil was just covered with water.

peregra he studied.[19] The latter snails may thus resemble our *ovata* from the shallow area. The habitat choices are also consistent with life-history differences between *peregra* and *ovata* from the stony shore; *ovata* reproduction was much more negatively affected in the laboratory when the water level was sinking than was *peregra* reproduction.[12]

As the *ovata* from the shallow area and *peregra* were collected from the same area, our results suggest that the habitat preferences are not entirely due to experience and so could be partially genetic. The simplest explanation for the intermediate preferences of *ovata* from the shallow area is that there is constant migration of *ovata* from the stony shore in this habitat. The large foot of *ovata* would certainly make such movements plausible.[10] The preferences of the offspring of such migrants would thus reflect both genetic and environmental influences. The disadvantage of the large foot under drying conditions, at least those as here which cannot be avoided by retreating into deeper water, would be increased water loss, and this could explain why the apparently superior competitor (it is overall much more common) cannot completely exclude *peregra* from the lake.

Thus habitat choice and field distribution appear to be closely related in *Lymnaea*. While substratum choice influences habitat choice, the likelihood that the habitat will dry temporarily seems to be the main explanation for the observed differences in microdistribution. Even weak habitat preferences and moderate fitness differences can lead to an appreciable divergence of populations,[20] which might explain why the forms do not hybridize to a greater extent.

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Trauma-induced, *in utero* hyperstrophy in *Melanoides tuberculata* (Müller, 1774)

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Hyperstrophy,[1] the presence of a sinistrally coiled shell in an anatomically dextral animal, or vice versa, (i.e.—with the apex of the shell on the same side of the body as the unpaired osphradium, ctenidium and heart), is a rare occurrence in Gastropoda. Larval shells of a number of heterobranch taxa, among them Architectonicidae and Pyramidellidae, are normally hyperstrophic, but, with few exceptions (e.g.—the pelagic, presumably neotenous *Limacina*), the direction of shell coiling changes at metamorphosis to produce dextrally coiled teleoconchs. There have been published reports of the abnormal retention of hyperstrophy beyond metamorphosis in architectonicids,[2] and of abnormal hyperstrophy in *Littorina lineolata* were the protoconch was orthostrophic, yet the teleoconch hyperstrophic.[3] Such individuals, however, are extremely rare.

In the course of a larger study of caenogastropod phylogeny, several juveniles intended for DNA extraction were removed from the brood pouch of a single adult specimen of *Melanoides tuberculata* collected at a depth of 1.5 m in a drainage canal in Loxahatchee, Florida. Since adult *M. tuberculatus* are hosts to a variety of trematode parasites, brooded specimens were used to minimize contamination of the DNA. Two of 31 juveniles from a single brood pouch were discovered to be hyperstrophic (Figs. 2–3). Closer examination of the early whorls revealed that both were originally dextrally coiled, and that the changes in the direction of coiling were associated with severe and repeated shell breakage (figures 6–7, arrows). It is surmised that the breakage occurred when the adult snail retracted suddenly into its shell, possibly to escape predation, and consequently compressed the numerous juveniles of widely varying sizes and stages of development against each other. The contents of the brood pouches of three additional *M. tuberculatus*, containing 18 to 71 juveniles, were examined. While repaired shell breaks were not uncommon among juveniles *in utero* (Fig. 5, arrow), no additional hyperstrophic individuals were found.

Robertson and Merrill[2] theorized that a possible cause of abnormal hyperstrophy might be 'an injury to the mantle of a larva,' but the absence of early whorls in the material before them precluded further study. Present observations indicate abnormal hyperstropy to be a deformity produced by repeated or severe trauma early in development rather than a congenital defect. Although such a deformity may not be less viable *in utero*, the rarity of hyperstrophic adults clearly suggests a greatly reduced post-larval survivorship.

A sinistral shell of *Melanoides tuberculatus* was recently reported from fossil beds in Israel.[4] The small size of this specimen (2.8 mm) falls well within the range of newly released juveniles,[5] raising the possibility that it may be dextral and hyperstrophic rather than sinistral.

Voucher material (preserved adults and an SEM stub with normal and hyperstrophic juveniles) is deposited in the collections of the National Museum of Natural History, Smithsonian Institution [USNM 888799]. I am indebted to Mr. Anthony Cinelli and Dr. Edward J. Petuch, both of Florida Atlantic University, for assistance in collecting these specimens.